NOTES AND LITERATURE

NOTES ON HEREDITY AND EVOLUTION

MENDEL, in his investigations, found certain *Hieracium* hybrids which did not split up in the second generation. The writer several years ago suggested that the cause of this phenomenon might be found in apogamy. Ostenfeld[1] has recently shown that in a large number of species of this genus apogamy exists. It therefore seems probable that the constancy of these hybrids is due to the omission of the reduction division.

Pearl and Surface[2] have recently published some very interesting contributions on inheritance as a result of studies of crosses made between Barred Plymouth Rock poultry and Cornish Indian Games. It was found that eggs produced by the cross Barred Plymouth Rock males on Cornish Indian Game females gave a larger per cent. of fertile eggs than the reciprocal cross; also a larger per cent. of fertile eggs than either pure breed produced. The low percentage of fertile eggs in the cross in which the Barred Plymouth Rock female was used, the authors suggest, may possibly be due to unfavorable environment for Cornish Indian Game spermatozoa in the Barred Plymouth Rock oviduct.

There was also a higher per cent. of fertile eggs hatched for the hybrids than for either pure breed, this result being attributed to the greater vigor of the hybrids.

The Barred Plymouth Rock breed is one which has high egg-laying quality, while the Cornish Indian Game has low egg-laying quality. The very interesting result was obtained that hybrids produced by using Barred Plymouth Rock sires were good layers, thus showing that the high laying quality was transmitted by the Barred Plymouth Rock sire. On the other hand, hybrids produced by using Barred Plymouth Rock females did not possess the high laying quality, thus indicating

[1] Ostenfeld, C. H., "Further Studies on Apogamy and Hybridization of the *Hieracium*," *Zeitsch. f. Induk. Abst.*, Vol. III, H. 4.

[2] Raymond Pearl and Frank M. Surface, "Studies on Hybrid Poultry," Annual Report, Maine State Experiment Station, 1910. See also *Arch. f. Entwick. d. Organ.*, XXX, p. 1.

that the Barred Plymouth Rock female does not transmit this quality directly. The facts appear to indicate that high egg laying quality is a sex limited factor like barring in the Barred Plymouth Rocks. Barred Plymouth Rock females would thus transmit high egg laying quality to their male offspring but not to their female offspring, while Barred Plymouth Rock males would transmit it to both sexes.

Shank color was also found to be a sex limited character. Both breeds have yellow shanks, though the Barred Plymouth Rocks sometimes have black pigment in the shank epidermis. In the cross Barred Plymouth Rock male on Cornish Indian Game female the progeny all have yellow shanks. In the reciprocal cross the male progeny have yellow shanks, while the female progeny have black shanks. The authors suggest that shank color behaves like barring in transmission. There is, however, evidently some difference, for here we get females showing a character not possessed by either parent. The writer would suggest, as a possible explanation of the behavior of shank color, that the chromosome which determines the female sex in the Barred Plymouth Rock probably has black shank latent and that this character is aroused into activity by the cross. The F_2 generation of this cross will probably give some important information on this point. Fortunately, these careful and indefatigable workers will continue these investigations.

In down color the hybrid chicks from the reciprocal crosses were alike but unlike either parent, being darker than the darkest parent.

The F_1 generation between pea comb (Cornish Indian Game) and single comb (Barred Plymouth Rock) gave all gradations from pea to single. There were more pea combs in some families than in others.

In body shape the males in the F_1 generation were all of the Cornish Indian Game type. The females were intermediate between the two breeds in this respect. The barred females—that is, those produced from Barred Plymouth Rock sires—were more like the Barred Plymouth Rock in body shape, and the black females more like the Cornish Indian Game.

In this paper the authors give the results of extended investigations relating to inheritance of the Plymouth Rock Barring. The paper is limited to the study of the cross between Barred Plymouth Rocks and Cornish Indian Games. The results con-

firm the present writer's hypothesis first published in 1908[3] concerning the method of inheritance of this character. The results obtained are consistent with the hypothesis that barring is allelomorphic to the female sex element. Thus, when male Plymouth Rocks are used in the cross only the male offspring are barred, the females being black. The plates accompanying the text show excellent illustrations of the nature of the barring, both in the pure bred Barred Rocks and in the hybrids. The hybrids are darker than the pure breeds, there being more pigment in the feathers.

Davenport has recently published an important contribution in the Carnegie Institution series on inheritance in poultry.[4] While he deals with many other characters than those relating to color, for lack of time to present an adequate review of the whole article, and because of its relation to the present subject, I give here only his results relating to color factors. The factors determined were as follows:

C = presence of color (absence of C gives albinism);
J = Jungle Fowl pattern and coloration;
N = super Melanic factor (nigrum);
X = super Xanthic or buff factor;
W = Graying (white) factor.

He found the Silkies and White Cochins both to be pure albinos having the gametic formula cJnwx.

White Leghorns were found to be grays with the formula CJNWx. This formula shows that W is an inhibiting factor which renders J and N invisible.

Black Minorcas and white-faced Black Spanish were found to have the formula CJNwx. In these breeds N obscures J, but the latter modifies the character black color.

Black Cochins were found to have the formula CINwx. In this formula I is a modification of J in which the pigmentation usually associated with J is absent.

Black Games were found to have the same formula as Black Cochins, but the pigment due to the factor N is less intense.

Buff Cochins were found to have the formula CjnwX. The author notes some variability in the degree of albinism, certain recessive whites showing specks of pigment. "The coloring enzyme may be absent to small traces."

[3] AMERICAN NATURALIST, Vol. 42, 1909, pp. 610–615.

[4] Davenport, C. B., "Inheritance of Character in Domestic Fowls," Carnegie Institution publication.

While the author recognizes sexual dimorphism as related to Jungle Fowl pattern, he does not work out the manner of inheritance of this factor. He probably would have done so had the birds been raised to the stage required for distinguishing this dimorphism.

Breeders of White Leghorns are frequently troubled by the appearance of a reddish sheen on the feathers. The formula of this breed gives a probable reason for this difficulty (CJNWx). It is probable that the Jungle Fowl coloration produces the effect in question. The cross between this breed and the Buff Cochin (CjnwX) gives an opportunity to get a breed of the formula CjnWx, which ought to be a pure dominant white, with no trace of coloration or pigment.

Goodale[5] has recently published a short but very interesting paper giving results of poultry breeding experiments, in which it appears that the Jungle Fowl pattern found in the Brown Leghorns, like the barring factor of the Barred Plymouth Rocks, is allelomorphic to the female sex factor. His paper also shows that while dominant white, when homozygote, is epistatic to black pigment, it is not so in the heterozygote condition of the white. It also indicates that females possessing the Jungle Fowl pattern and having Plymouth Rock white and Plymouth Rock black pigment, both in the heterozygote condition, may vary in color from black to almost typical Brown Leghorn pattern.

The progeny of females obtained by mating Brown Leghorn females with white Plymouth Rock males show no trace of the Jungle Fowl pattern or color, while the males obtained from this cross transmitted the Jungle Fowl pattern. There is opportunity here for a very interesting study. If the Jungle Fowl pattern and the barring of the Plymouth Rocks are both allelomorphic to the female sex factor, it would be very interesting to ascertain whether females can have both of these factors present in them. If so, it would show either that the female sex factor itself may be coupled with one or the other of these factors, or that the allelomorph to this factor may contain both factors coupled, or that the two factors reside in separate chromosomes both of which behave as allelomorphs to the female sex chromosome.

Castle has recently shown[6] that Miss McCracken's results in

[5] *Proc. Soc. Exp. Biol. and Med.*, Vol. 7, No. 5, May 18, 1910.

[6] Castle, W. E., *Jour. of Exp. Zool.*, Vol. 8, No. 2, March, 1910.

univoltinism and bivoltinism[7] are not inconsistent with Mendelian theory. The difficulty in interpretation is due to the fact that the characters in question are exhibited by one sex only. The same difficulty arises in following out the cross between white and red corn, since red shows only as an internal character.

Hagedoorn,[8] in mating an albino mouse having the barring (agouti) character with a homozygous yellow female, finds the barring and the yellow color to be allelomorphic to each other. Certain yellow individuals mated to black gave only yellow offspring. It is probable that the yellow contains an inhibiting factor for black. Other yellow mice of a different shade mated to black gave black young. His results confirm those of Goodale in that he finds the bankiva pattern and color in Bantams crossed with Brown Reds to behave as if the bankiva pattern were allelomorphic to femaleness. When females of the bankiva type were used in the cross the male offspring were all bankiva and the females all Brown Red. When the cross was made in the opposite direction both sexes were of bankiva type. He also found (page 26) some bankiva females apparently homozygous for bankiva pattern. His data are not full or complete on this point.

On page 29 he reports that the cross between *Primula sinensis* and *P. stellata* gives *P. pyramidalis*. F_2 from this cross gives 25 per cent. *sinensis*, 25 per cent. *stellata*, and 50 per cent. *Pyramidalis*, although the two parent forms differ in more than one respect, the differences apparently being coupled.

The writer has frequently suggested that if a careful search were made for more cases of what Bateson has termed "false allelomorphs" they might be found to be more abundant than they are thought to be. Those cases which have been discovered show that such phenomena are not discovered usually unless one is looking for them. We have now a considerable number of cases of sexual dimorphism in which some somatic character acts as an allelomorph to femaleness. Presumably, these sex-limited characters would act as allelomorphs to each other if brought together in the same zygote. We have already referred to the barring of Plymouth Rocks and to the Jungle

[7] *Jour. of Exp. Zool.*, Vol. 7, No. 4.

[8] Hagedoorn, A. L., "Mendelian Inheritance," *Arch. f. Entw. d. Organ.*. Vol. 28, H. 1.

Fowl pattern as instances of this kind. When Silkies are crossed with Brown Leghorns, the latter breed introduces an inhibiting factor for the intense black pigmentation in the flesh of the Silkies, and this inhibiting factor appears to behave as if it were allelomorphic to femaleness. The inheritance of the factor is not yet fully worked out.[9] In addition to these cases we have that of melanism in *Abraxas grossulariata* when crossed with *A. lacticolor*. Black eyes in canaries when crossed with pink eyes appear to behave in a similar manner. We have already mentioned above shank color in poultry in this connection.

Dr. R. A. Gortner, of the Station for Experimental Evolution, Cold Spring Harbor, New York, in THE AMERICAN NATURALIST for August, 1910, gives results of quantitative determinations of melanin in white wool and black. He finds 1.84 per cent. in black wool and only .06 per cent. in white. He expresses the opinion that the melanin in white is a decomposition product of keratin and not a true melanin, thus disproving Riddle's assumption that dominant white is a more advanced stage of oxidation than black. He advances the theory that dominant whites are due to the presence of an anti-oxidase which prevents pigment formation, while recessive whites have neither power to form pigments nor to inhibit the formation.

Ostenfeld[10] finds that the number of chromosomes in the apogamic race of *Rosa canina* is about double the number in the normal sexual race in the same species, thus indicating that the reduction division is omitted.

It has generally been supposed that when an organism is moved from one environment to another distinctly different, there is a tendency for the type to break up. This thing has been described as "new place effect." There has been very little investigation bearing directly on this question, and most of it has related to forms more or less mixed in inheritance rather than to pure lines of the same inheritance. Data bearing on this subject are important and very much needed. An important contribution to our knowledge of the subject is found in Bulletin 128 of the Bureau of Chemistry of the U. S. Department of Agriculture. In this bulletin LeClerc and Leavitt give the results of experiments on wheat. Kubanka Wheat grown

[9] "Bateson's Mendelian Principles of Heredity," pp. 81–87.

[10] *Zeitsch. f. Induk. Abst. und Vererb.*, Bd. III, H. 4, May, 1910, p. 253.

in South Dakota was distributed to stations in Kansas and California. Each year a sample from each station was sent to each of the others and grown there. A similar series of experiments was conducted with Crimean Wheat in Kansas, Texas and California. The results may be briefly stated as follows.

The same variety of wheat when grown at the same station, no matter what the source of the seed, showed the same characteristics, but the same variety grown at different stations showed marked differences. This result was obtained in the case of both varieties. These results are in entire accord with the results on barley secured by Dr. Albert Mann, who grew pedigree seeds of barley at a large number of stations in this country. The original seed was from Svalöf. These results have been previously referred to in these notes.

The appearance of an English edition of de Vries's "The Mutation Theory" (Vol. I)[11] gives the opportunity for many non-German readers to gain first hand knowledge of this remarkable work. It also serves to show the truly wonderful progress that has been made in the study of the phenomena of evolution since this book was originally published (1901–03).

In reading this book one can not fail to be impressed with the current misconceptions concerning its teachings. De Vries's disciples have given the phrase "discontinuous variation" a meaning quite different from that in which it is used in "The Mutation Theory." By "continuous" variability de Vries means the kind that fluctuates about a norm and thus presents a continuous series of modifications. Illustrations of continuous variability in this sense are found in ordinary fluctuating variations within pure lines. It was Quetelet who first discovered the fact that ordinary fluctuating variability gives a continuous series of variations varying in frequency inversely with their magnitude. That is, the magnitude of a given variation of this kind is governed by the ordinary laws of probability. In such variation every degree of departure from the normal is found. On the other hand, if we study a given character in a complex Linnean species consisting of several pure strains or subspecies, we find that each of the pure strains gives us a case of continuous variation—*i. e.*, of "fluctuation" about a norm which is fixed. But if we take these norms for a large number of pure

[11] de Vries, Hugo, "The Mutation Theory," Vol. I, The Open Court Publishing Co., Chicago, Ill., pp. 575.

strains within a species and attempt to arrange them in a frequency polygon, we find gaps not represented in the series, at least in some species. This kind of variation de Vries calls "discontinuous variation." We can all agree that there are such gaps between related forms in many cases. Thus, if we adhere to the original use of the term "discontinuous variation," there is no chance for debate about it. It is simply a name given to a series of well ascertained facts. How these gaps came into existence is another question. The change in the use of the term which has occurred since "The Mutation Theory" was written is in its application to the method by which these gaps came to exist rather than to the fact of their existence.

A careful consideration of the data now at hand seems to the writer to leave little question that there are gaps between related forms which came into existence suddenly, and thus represent discontinuous variation in the more modern sense of this term. The only dispute which seems to the writer justifiable relates to the question whether all permanent evolutionary change comes about in this manner; and this question will be brought up again later in this article.

The progress made since "The Mutation Theory" was published is illustrated by the fact that in this book de Vries takes no account of the pure lines differing quantitatively with reference to a given character, such as those studied by Jennings, Johannsen, Nilsson-Ehle and others. De Vries also adheres throughout the book to the old notion that a given character can be modified quantitatively by selection, and states on page 51 that "It is to the selection of the material afforded by individual variability [fluctuation] that the origin of many improved races is due." Many other similar statements occur in the text. Recent investigations have thrown much doubt on the correctness of this view; we may say, have disproved it. All the recent careful work on the subject points to the opposite conclusion.

While in this book de Vries sets forth very clearly the idea that his "individual variation" is what we now call fluctuation, he continually confuses fluctuation with the effect of crossing. For instance, on page 100, we find the following: "All this [improvement of the sugar beet] has been done by selection of the best individuals afforded by ordinary fluctuating variation. Neither spontaneous variations nor crossings have played any

part in it. We are dealing here with the process in its simplest form.'' It is far from demonstrated that crossings have had nothing to do with the improvement of the sugar beet. The consensus of opinion of most biologists at the present time is that selection can accomplish nothing except the isolation of the best strain or best Mendelian combination existing in a given population. It is hardly fair, however, to attribute to de Vries the opinions expressed ten years ago, for he would probably hold to-day that the opinions expressed concerning the effect of selection in ''The Mutation Theory'' have been proved to be incorrect. Such a position is really more in keeping with the fundamental principles involved in his theory, and I have no doubt that de Vries would fully admit that selection can not affect fluctuating variability, or at least that all of the recent evidence points in this direction.

For the purpose of discussing de Vries's fundamental theorem we may classify the various types of variation as follows: (1) Fluctuation; (2) those due to Mendelian recombinations; (3) those due to change in personnel of the chromosomes or other cell organs having a relation to ontogenetic development; (4) those due to fundamental changes in whatever material is responsible for the metabolic activities which result in development.

Fortunately, at the time ''The Mutation Theory'' was written the general facts of Mendelian recombination were recognized and are taken into account by de Vries, though, as previously stated, he frequently confuses them with other types of variation. De Vries also recognizes fluctuation, which he describes by the term ''individual variability,'' and appraises it at its true value, except, as stated above, that he credits selection with the power of producing temporary modifications by means of it.

The last two types of variability were not recognized when ''The Mutation Theory'' was written, so that they are utterly confused in this book.

Before de Vries undertook his Œnothera studies he was already committed to a theory concerning the manner in which evolutionary changes come about, and frankly states that his work was undertaken in order to find confirmation of this theory. Strangely enough, Darwin was responsible for the fundamental idea underlying de Vries's theory of mutation. It will be remembered that in attempting to explain the sup-

posed inheritance of acquired characters Darwin formulated the theory of pangenesis, according to which each cell in the organism gives off a bud, or gemmule, which migrates to the germ plasm and in the next generation becomes responsible for the development of a corresponding cell in the new organism. De Vries drops the idea of migration of the gemmules from the organism into the germ plasm, and starts with these gemmules as permanent constituents of the germ plasm. He also makes other modifications in the nature of these bodies, and hence very properly gives them a new name, "pangenes."

I am of opinion that had de Vries taken an agricultural variety of wheat for his studies he would have been led to the development of a different theory. Unfortunately, he found the mutations for which he was looking in a species which was throwing off variants in a manner which we may well believe to be unusual. In fact, de Vries examined over a hundred species before he found one that suited him in this respect. Recent cytological investigations by Gates, Miss Lutz and others seem to justify at least the tentative assumption that the *Œnothera* mutants arise from a change in the personnel of the chromosomes. It is certain that in *Œnothera gigas* the *Lamarckiana* the number of chromosomes has been doubled. Gates has shown that in a general way the nuclei in *gigas* cells are twice the size of those of *Lamarckiana.* Other mutants have numbers of chromosomes not exactly corresponding with Lamarckiana. It is also demonstrated that in *Lamarckiana* and several of its mutants the course of events in the reduction division is abnormal. A good many of the chromosomes do not unite into bivalents in the usual manner, thus giving opportunity for all kinds of irregularities in the distribution of the chromosomes. The further fact that many of the mutants produce only a small proportion of functional gametes at least suggests that in many reduction divisions the chromosomes are distributed in such a way as to interfere with the future development of the gametes and the zygotes which would be formed from them.

If we assume that the chromosomes, because of their relation to the processes of nutrition or for other reasons, have an important influence on the course of development, and that there are irregularities in the distribution of these bodies in the reduction division in *Lamarckiana* and its offshoots, we at once find a satisfactory interpretation of the behavior of these mu-

tants, and we can easily see how de Vries was misled by his material. He got the idea that the organism is composed of distinct and independently heritable units and that when one of these units is lost out or when a new one springs into existence we get an organism which differs in all of its characters from the parent form. He assumes that all permanent evolutionary change comes about by the introduction of new pangenes. For instance, he says:

> The contrast between these two groups of phenomena, variability (in the strict sense) [fluctuation] and mutability, becomes obvious when we imagine that properties of organisms are built up of perfectly distinct and independent units. The origin of a new unit is a mutation.

Again on page 57:

> Elementary species and forms closely allied to them are distinguished from one another not by a single feature but by all their organs and peculiarities. The difference between closely allied forms often demands long and extensive diagnosis. Nevertheless this diagnosis must be regarded as an expression of a single character, a single unit, which arose as such, and as such can be lost.

Again, on Page 61: "By mutation new characters arise all at once"; and on page 63: "Each mutation is a definitely circumscribed unit."

De Vries overlooks entirely those closely related pure lines, differing frequently only quantitatively, and in a single character, which to the writer represent what may be called normal evolutionary change. They not only do not differ in all their characters as the *Œnothera* mutants do, but their norms present a regular series coming under Quetelet's law, and thus represent "continuous variation," as de Vries defines it. Yet they are undoubtedly of true evolutionary value. Of these types Jennings says:[12]

> The work with genotypes [pure lines] brings out as never before the minuteness of the hereditary differences that separate the various lines. These differences are the smallest that can possibly be detected by refined measurement taken in connection with statistical treatment.

And again on page 145:

> That smaller hereditary differences are not described is certainly due only to the impossibility of more accurate measurements. Genotypes

[12] AMER. NAT., XLIV, pp. 144–145.

so differing have not risen from each other by large mutations. The genotype work lends no support to the idea that evolution occurs by large steps, for it reveals a *continuous series*[13] of the minutest differences between great numbers of existing races.

Nilsson-Ehle, in dealing with genotypes of oats, shows that the related lines can be arranged in a Quetelet curve with respect to the average length of the flowering glume,[14] as follows:

Average length of hull mm.	Number of genotypes
14–15	2
15–16	16
16–17	38
17–18	14
18–19	2

It would be difficult to imagine a better case of "continuous variation," as defined by de Vries.

To the writer it seems there can be no doubt that the type of variation illustrated by these pure lines of oats, and by the many pure lines of *Paramecium* studied by Jennings, is altogether different from that studied by de Vries, and is due to a widely different cause. In the writer's opinion, the *Œnothera* mutants are due to irregularities in the distribution of chromosomes in the reduction division, while the hereditary variations of the *Paramecium* type are due to actual changes in function (increase, decrease) of cell organs that have a relation to development. When such changes occur in the functions of chromosomes, the resulting differences obey Mendel's law; when they occur in other cell organs they do not obey this law.

De Vries simply generalized from too small a range of phenomena. There can be very little doubt that had he worked with the numerous small differences that exist in many species, such as have been the subject of later studies by others, he would have come to a different conclusion, or would have at least greatly modified his conclusions. The work with genotypes certainly points to a different cause for evolutionary change from that assigned by de Vries. Had he recognized what we may call the *Paramecium* type of mutation he certainly would not have said (p. 155):

> The assumption that human variability bears any relation to the variation that has or is supposed to have caused the origin of species

[13] Italics mine.

[14] *Bot. Not.*, 1907, pp. 113–140.

is to my mind absolutely unjustified. . . . Since the beginning of the diluvial period man has not given rise to any new races or types. He is, in fact, immutable, albeit highly variable.

But even those of us who do not believe that *all* evolutionary change is saltatory, as it seems to be in the *Œnothera* mutants, can agree with de Vries that the difference between fluctuation and mutation lies in the fact that fluctuation is due to environment and is not hereditary, while, when a step has actually been accomplished in permanent evolutionary change, the norm about which fluctuation occurs is different from the old one. We can accept this doctrine even if we deny that the difference between the new and the old is not a "unit." We can not, however, accept the idea, repeatedly brought forward in this book, that "There is no question that improvement takes place in the experimental garden" (p. 110) when selecting for improvement in pure lines, or when he says "In the case of no single character can selection be relaxed" (p. 106); or when he quotes Halley (p. 111), with approval, to the effect that in improving wheat by selection, "the rate of improvement gradually falls off year by year until at the end of many years the race reaches a maximum and becomes constant. But, of course, it will not remain so if it is not subjected to continuous selection."

W. J. Spillman.

(*To be continued.*)